Giraffe (*Giraffa camelopardalis*) social networks in areas of contrasting human activity and lion density

Giraffe networks, human activity and lion density

Zoe Muller.[1,2*], Innes C. Cuthill[1], Stephen Harris[1]

[1]School of Biological Sciences, Life Sciences Building, University of Bristol, 24 Tyndall Avenue, Bristol BS8 1TH, UK.

[2]Giraffe Research & Conservation Trust, PO Box 1781 – 00606, Nairobi, Kenya

* Corresponding author: Zoe Muller, muller.zoe@gmail.com

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Abstract

The adaptive value of close social bonds and social networks has been demonstrated in a variety of vertebrate taxa. While the effect of predators on populations is well established, disturbance by humans is increasingly being identified as affecting the behaviour and reproductive success of animals and can have significant impacts on their survival. We used a concurrent analysis of two adjacent giraffe *Giraffa camelopardalis* populations in Kenya to determine whether human activities and high predation affected their social networks. One study site was a premier tourist destination with a high volume of human activity in the form of tourist traffic and lodge infrastructure, alongside a high density of lions which preferentially prey on giraffe calves; the other was a private wildlife conservancy with minimal human activity and no lion population. Giraffes in both networks showed preferred associations and avoidances of other individuals, which were independent of space use. Bond strength was lower in the population exposed to high levels of human activity and lions, and the network had lower density and clustering, and shorter path lengths, suggesting that it was more fragmented. We suggest that human activity and predator density may influence the patterns of social interactions in giraffes and highlight the importance of understanding the impact of tourism and management on the survival and success of wild animal populations.

Keywords

Giraffa camelopardalis, human disturbance, predation, predator density, social behaviour, social bonds, social networks, wildlife tourism

1 INTRODUCTION

The effects of predator presence on the behaviour of African ungulates are well established (Valeix et al. 2009a, b; Périquet et al. 2010; Creel et al. 2014; Ripple et al. 2014); however, there has been limited investigation into how these behavioural changes may influence the structure of social organisation of prey species, or the changes in network structure. Since social networks offer fitness benefits and may influence an individual's survival (Silk 2007a, 2009; Brent et al. 2015; Goldenberg et al. 2016) and risk of disease (Drewe 2009; MacIntosh et al. 2012; VanderWaal et al. 2014a; Adelman et al. 2015), understanding how the social organisation of prey species responds to predation risk is an important, yet almost completely neglected, area of biology. Furthermore, it is well recognised that populations of African mammals are in decline (Craigie et al. 2010; Ogutu et al. 2011; Ceballos et al. 2017), yet there is also an increasing appetite and economic justification for tourism in protected areas (Beale & Monaghan 2004), which is likely to impose significant disturbance on populations of resident animals (Green & Giese 2004; Kerbiriou et al. 2009). Given that disturbance by humans through tourism is increasing, it is critical that we understand how such disturbance affects the social organisation of animals to ensure species protection and balance this with the increasing economic justification for tourism in protected areas (Beale & Monaghan 2004). In this paper, we present a population-level analysis of the social organisation of an African ungulate species with variable social organisation, the giraffe *Giraffa camelopardalis*, comparing two adjacent populations exposed to different levels of human activity and density of lions.

Fission-fusion social organisation, whereby group size and composition are constantly changing, characterises many taxa and is considered to be an adaptive response to changing environmental conditions (Green & Giese 2004; Aureli et al. 2008). Such a flexible social system is likely to have arisen as animals seek to balance the costs and benefits associated with grouping (Krause & Ruxton 2002). Social bonds are considered to be a product of these trade-offs, whereby individuals gain benefits from associating with or avoiding other individuals (Palombit et al. 1997; Connor et al. 2000;

74 Silk 2007b); close bonds provide benefits such as enhanced infant survival (Silk et al. 2009),
75 increased lifespan (Silk et al. 2010), lower stress levels (Crockford et al. 2008; Wittig et al. 2008) and
76 reduced levels of aggression within groups (Haunhorst et al. 2017). Despite the prevalence of fission-
77 fusion social organisation in animals, and a large body of research investigating the causes, costs and
78 benefits of different patterns of social organisation, the conclusions about what drives social
79 structure remain highly variable (Patriquin et al. 2010). Even for the same species, different studies
80 reach different conclusions, demonstrating the highly responsive nature of networks to local factors
81 (Leu et al. 2016).

82 Most animals do not exist in isolation and so it is beneficial to consider social organisation at a
83 network level (Whitehead 2008). The application of network theory to the study of animal social
84 organisation has allowed rapid advances in our understanding of population-level behaviour (Krause
85 et al. 2007; Kurvers et al. 2014; Brent et al. 2015). A social network approach is useful because it
86 provides a validated, quantitative approach to characterise both individual- and population-level
87 social structure (Krause et al. 2007). Studying the social network of populations allows greater
88 insight and understanding of processes which support disease transmission (VanderWaal et al.
89 2014a; Mejía-Salazar et al. 2017), social learning (Hobaiter et al. 2014), and the evolution of social
90 strategies (Cameron et al. 2009; Brent et al. 2015).

91 The environmental factors affecting fission-fusion organisation in mammals include climate,
92 resource availability and distribution, predation risk, group size and human influences (Lehmann &
93 Boesch 2004; Couzin 2006; Lehmann et al. 2007; Sundaresan et al. 2007; Aureli et al. 2008; Kelley et
94 al. 2011), but the factors influencing fission may differ from those driving fusion. For example, in
95 African elephants *Loxodonta africana*, fission events are driven by resource availability and
96 distribution, but fusion events are influenced by genetic relatedness (Archie et al. 2006, 2008; Chiyo
97 et al. 2011). Variation in the effects of environmental variables on patterns of social organisation
98 have also been found in brown bats *Eptesicus fuscus* (Willis & Brigham 2004; Metheny et al. 2008),

meerkats *Suricata suricatta* (Drewe et al. 2009; Madden et al. 2009), bottlenose dolphins *Tursiops truncatus* (Parsons et al. 2003; Möller & Harcourt 2008; Frère et al. 2010), chimpanzees *Pan troglodytes* (Lehmann et al. 2007; Langergraber et al. 2009), red ruffed lemurs *Varecia rubra* (Vasey 2007) and humans *Homo sapiens* (Marlowe 2005).

Disturbance by humans is increasingly being recognised as having significant effects on the behaviour and reproductive success of animals (Manor & Saltz 2003; Green & Giese 2004; Hebblewhite et al. 2005; Stankowich 2008; Bonnot et al. 2013) and can adversely affect the survival and management of wild populations (Carney & Sydeman 1999). Numerous studies have found that human activities can disrupt breeding (Giese 1996), influence mortality rates (Feare 1976; Wauters et al. 1997) and scare animals away from preferred feeding sites (Gander & Ingold 1997). How human disturbance influences social behaviour at a population level has been less well studied, but is likely to be associated with the disruption or prevention of natural behaviours. To date, few studies have used a network approach to investigate how human activity influences the structure or function of animal social networks. However, a study of how human activity affects the social bonds of spotted hyaenas *Crocuta crocuta* found that clans in areas with high levels of human activity showed lower density (less connectivity in the network), suggesting weaker social bonds (Belton et al. 2018). The disruption of typical social structures may have important fitness implications for individuals, but it is not clear how human activity influences these processes. Likewise, the impact of predators on populations of prey species is well documented (Ripple & Beschta 2003; Creel et al. 2014), but it is not clear how predator density might influence social organisation at a population level. Only one previous study has attempted to quantify the effects of predation on network structure; the authors studied guppies *Poecilia reticulata* in a lab system (Kelley et al. 2011). They found that under predation, networks were higher in strength and connectedness, and individuals had more associates, than fish and networks under a low risk of predation. Groups under high predation risk also stayed together for longer, while groups under low risk disbanded more regularly (Kelley et al. 2011).

As a large, conspicuous fission-fusion species, giraffes present the ideal opportunity to study social structure dynamics. Social network methods have highlighted their non-random patterns of association (Bercovitch & Berry 2013a; Carter et al. 2013a, b; Malyjurkova et al. 2012), although there is no clear consensus on many aspects of giraffe social behaviour, and network structure has yet to be linked to fitness in this species. That said, one study has highlighted how the social network of giraffes influences their risk of exposure to pathogens (VanderWaal et al. 2014a). Giraffes inhabit a wide variety of landscapes and habitats throughout eastern and southern Africa, and their fission-fusion social system potentially allows them to adapt their behavioural strategies to local environmental differences.

Giraffe populations exist in a wide range of habitats, from deserts to woodland and savannah environments, and mean group size ranges from three to nine, depending on season, location and availability of conspecifics (Muller et al. 2018a). However, most studies examining social behaviour in giraffes focus on single, isolated populations, making it difficult to draw general conclusions about this species' behavioural ecology. Comparing same-species networks under differing environmental conditions is an important tool in developing greater understanding of mechanisms underlying collective and social behaviour (Voelkl & Noë 2008; Sueur et al. 2009, 2011), although this is currently lacking for giraffes. Given that predator density influences the population demography of giraffes (Muller 2018) and that population demography has a strong influence on patterns of social organisation (Faust 2006; Flack et al. 2006; Silk et al. 2006; Williams & Lusseau 2006; Kanngiesser et al. 2011), we suggest that general conclusions drawn from single-population studies must be interpreted with caution, since these results may represent how a specific social network responds to a particular set of circumstances that are not generalisable to other populations.

In this study, we aim to examine the effects of disturbance on the social network structure of giraffes. We compare two populations of wild giraffes, each subjected to different levels of disturbance by human activity and predator presence. One population was classified as being under

'high disturbance' and the other under 'low disturbance' (see Methods for justification). We compare two aspects of sociality between the populations: first, the motivation to bond with conspecifics, and second, how the results of bonding are manifested within the social network. The two available studies investigating network changes under predation (Kelley et al. 2011) and disturbance by humans (Belton et al. 2018) found varied results, so it is difficult to use these studies to predict what may happen in giraffes exposed to both pressures. However, given the evidence that disturbance by tourism disrupts normal group behaviour in animals (Green & Giese 2004; Lusseau & Bejder 2007; Ranaweerage et al. 2015), we predict that the social network of giraffes exposed to high levels of disturbance will be more fractured, and we test four hypotheses. High levels of disturbance will lead to i) lower bond strength, ii) lower density, as individuals disband following disturbance, iii) a lower number of sub-communities representing a more fractured society, and iv) shorter path length as individuals move around more due to high levels of disturbance by humans.

Comparing two different wild populations presents several challenges since there are multiple factors which can vary between them, but they also present an opportunity to begin to understand the relative influence of different variables on social organisation. Performing a concurrent analysis of two populations has great value, especially if the populations are close and data collection and analytical methods are kept consistent (Farine & Whitehead 2015); this is the approach we take here.

2 METHODS

All experimental protocols and procedures employed in this study were approved by the University of Bristol Animal Welfare and Ethical Review Board (project number UB/11/003), the Kenya National Council for Science and Technology and the Kenya Wildlife Service.

2.1 Study areas

We studied two populations of Rothschild's giraffes *Giraffa camelopardalis rothschildi*; one was enclosed within Soysambu Conservancy (SC) and one was enclosed within Lake Nakuru National Park (LNNP), both of which are located south of Nakuru, Kenya between 00°22'S and 36°23'E. SC is a private wildlife conservancy (size 190 km^2, 1670 m asl) surrounding Lake Elementeita; LNNP is a National Park (size 188 km^2, 1759 m asl) surrounding Lake Nakuru. The two study sites are adjacent with a shared 7.8 km boundary along the west fenceline of SC and the east fenceline of LNNP (Figure 1). An electrified game fence, across which no large mammals could pass, was a physical barrier between the two study sites. The climate, topography, soil types, vegetation and the diversity of flora and fauna found in each area are similar and they are part of the same biome and microclimate (Nicholson 1996; Omondi 2011).

There are two notable differences between the study sites: (1) the density of lions, *Panthera leo,* and (2) the levels of human activity. Lions are the only predator to pose a significant threat to giraffes (Hirst 1969; Pienaar & De 1969; Foster & Dagg 1972; Dagg & Foster 1976; Strauss & Packer 2013). At the time of this study, LNNP contained 56 lions (Ogutu et al. 2012), which is a high density (0.3 lion/km^2) compared to more typical densities of 0.08 to 0.14 lion/km^2 (East 1984; Creel & Creel 1997). Preferential preying of lions upon giraffes has been identified as a problem in LNNP, along with observations of lions feeding on giraffe calf carcasses in the park (Kenya Wildlife Service 2002; Brenneman et al. 2009). During the same time, SC was free of lions and had been for several decades (Hugh George Cholmondeley, owner of Soysambu Ranch, personal communication). Additionally, the levels of human-related disturbance also varied between sites; LNNP is classified as a 'Premium Park' (Maingi et al. 2016) and is the second largest revenue-producing National Park in Kenya. In 2012 it received 253,500 visitors (Muthoka et al. 2017). It has an extensive road network, contains five large tourist lodges and several campsites. In contrast, SC is a privately owned and managed conservation area, which changed its main use from a private cattle farm to a wildlife conservation area in 2009. It was an under-utilised area for ecotourism (Kenya Wildlife Service 2004) and received significantly fewer visitors per year than LNNP. At the time of this study, there was an

201 average of 1 tourist vehicle per day in SC (Z. Muller, personal observation), the area had a limited
202 road network and no tourism infrastructure.

203 To acknowledge differences in predator density and levels of human activity between sites, and
204 because we could not discriminate between effects of predation and human disturbance with only
205 these two populations, we used more general descriptions of 'low disturbance' for SC and 'high
206 disturbance' for LNNP. We accept that we were unable to quantify predation risk in each population,
207 but human-related disturbance and tourism can be considered a form of predation risk (Frid & Dill
208 2002; Amo et al. 2006; Geffroy et al. 2015). Furthermore, high levels of human activity have been
209 shown to alter the structure of networks (Belton et al. 2018), which supports our decision to refer to
210 the two populations in terms of varying levels of disturbance.

211

212 2.2 Data collection

213 We carried out a three-month pilot study in each site (SC: March-May 2010; LNNP: March to May
214 2011) to identify, sex and age all individuals, and to develop an appropriate definition for 'group'.
215 We also used this time to determine a distance threshold in which giraffes could be approached by
216 vehicle without being alarmed by our presence; this was typically 100 m – 500 m. Giraffes were well
217 habituated to the presence of vehicles, and we took care to respect this distance threshold during
218 data collection so as not to influence their natural behaviour. However, it was not necessary to get
219 so close to groups since we used a zoom lens to obtain digital photographs of group members, and
220 binoculars to verify numbers, so data were usually collected from a much greater distance than the
221 'disturbance' threshold (typically >500 m to 1 km, depending on road layout and visibility). Following
222 the pilot study, data were collected for nine months in each study site (SC May 2010 – January 2011;
223 LNNP May 2011 – January 2012). All giraffes were individually identified (ID) using unique coat
224 patterns (see Muller (2018) for full details of ID methodology and site map). Each study site was
225 segmented into quarters. Giraffes were searched for by driving transects along the road network in

226 each area, using a 4x4 vehicle. All areas (i.e. the entire study site) were searched each day. Roads
227 taken and direction driven were randomised. Data collection started at 06:30 hrs and ended at 18:30
228 hrs (UTC + 3 h Standard Time). Upon sighting an individual or group of giraffes the vehicle was
229 stopped at an appropriate distance so as not to influence their behaviour. There is no standard
230 definition of group size for giraffes. Previous studies use either inter-individual distance thresholds,
231 which ranged from 100 m (Jeugd & Prins 2000), through 400-500 m (Leuthold 1979; Carter 2013;
232 VanderWaal et al. 2014b), to 1000 m (Foster 1966; Pratt & Anderson 1985), or similarity of
233 behavioural state (Backhaus 1961; Shorrocks & Croft 2009). However, a common theme was that
234 giraffe groups are self-defining; distances within groups are substantially smaller than distances
235 between groups (Shorrocks & Croft 2009; Carter 2013; VanderWaal et al. 2014b). During the pilot
236 phase we also found that groups were self-defining; the proximity of individuals within a group was
237 typically up to 200 m, but inter-group distances were always above 1 km. We also noted that group
238 members typically were synchronised in their behaviour. Therefore, we set the definition of a group
239 as 'all individuals within 1 km of each other and engaged in generally similar behaviour'. The
240 individual ID of all group members was recorded. We sampled each group for exactly 30 min to
241 standardise observation time between groups and ensure that all members of the group had been
242 recorded. We categorised each data point using a 'reliability score' of 1: certain that all group
243 members had been observed; 2: unsure if all group members had been observed; or 3: certain that
244 all group members had not been observed. Only data points of score 1 were used in the analyses to
245 ensure complete accuracy of identifications of group membership. Data reliability score was not
246 influenced by habitat type or complexity; there were equal proportions of scores for each habitat
247 type/complexity. All methods and the data collection procedure were standardised between sites to
248 ensure consistency and comparability of data sets. At the time of this study, SC contained 77
249 giraffes: 26 females, 25 males and 26 calves (individuals < 1 year), and LNNP contained 89 giraffes:
250 44 females, 40 males and 5 calves (Muller 2018).

251 2.3 Social network analysis

Data from each population were analysed separately, since each network was discrete with no migration between populations. Associations were defined using the gambit of the group, whereby all individuals within a group were said to be associated (Croft et al. 2008) and associations were symmetrical (i.e. if A is associated with B, then B is also associated with A). We created an adjacency matrix (an NxN matrix describing the edges in the network) for each site and populated this with the pair-wise associations observed between each pair of individuals. The pair-wise associations (edge weights, or cell values in the adjacency matrix) were calculated using the Simple Ratio Index (SRI) (Cairns & Schwager 1987; Whitehead 2008; Hoppitt & Farine 2018), which estimates the proportion of time that two individuals spent together. We calculated the SRI using the formula: SRI = $X / (Y_A + Y_B - X)$, where A and B are individuals in a dyad, Y_A and Y_B are observations of individuals A and B respectively, and X is the interactions between A and B. The SRI accounts for sample size and number of observations of each individual and provides a quantitative measure of the frequency of co-occurrence while also controlling for effort: 0 indicates animals that were never observed together and 1 indicates animals always observed together (Whitehead 2008)). To quantify bond strength between individuals (hypothesis i), we examined i) the mean edge weight i.e. SRI value describing strength of association between two individuals, and ii) the coefficient of variation (CV) of edge weights for all individuals in the network. High SRI and CV values represent focused association with specific individuals, i.e. individuals with high SRI and CV values have few, preferred associates (strong bonds). Low SRI and CV values represent more non-specific patterns of association, where individuals associate more freely with a wider set of conspecifics (weaker bonds) (Whitehead 2008; Leu et al. 2016).

Since there were differences in the calf cohort between the two study sites (Muller 2018), we ran the analyses twice for each population, once on the whole network and once on a filtered network which excluded calves, to understand the influence of demography on the network. We did this to mitigate the effects of demographic differences between the two sites, to understand the possible influence of different proportions of calves in each network, and because calves are unlikely to

contribute towards adult grouping decisions (Cameron & du Toit 2005; Muller et al. 2018a). That said, exclusion of calves does not remove the effects of their presence on adult decisions.

We calculated further measures to quantify properties of other elements of the network. Density (hypothesis ii) is the number of observed associations in a network, divided by the possible number of associations (Farine & Whitehead 2015). A low density score indicates that few individuals associate within social groups (Madden et al. 2009), while a high density score indicates that many of the possible associations have occurred, and animals are highly social among and between groups. Density is standardised by the maximum weight in the network, and is calculated based on the frequency of the interactions within the network (Whitehead 2008). To test hypothesis iii, we calculated clustering coefficient, which measures the extent to which an individual is connected to other individuals. It describes how many cliques are in a network: high clustering coefficient values indicate highly connected groups of individuals (Newman 2003; Whitehead 2008). To test hypothesis iv, we calculated path length as a measure of how connected or separated each individual is. Path length quantifies the number of edges connecting a pair of nodes, i.e. how many individuals are required to connect two non-directly connected individuals (Wey et al. 2008). We used weighted path lengths, which accounts for the SRI values between individuals in the network. All analyses were done in R (R Core Development Team 2017) using the asnipe (Farine 2013) and igraph (Csárdi & Nepusz 2006) packages.

2.4 Statistical significance testing using permutation tests

Due to the non-independent nature of network data, null models were used as a way of testing hypotheses. Null models use observed networks to randomly generate comparable networks containing the same number of nodes and edges, and replicate observed patterns of association, but without the process of interest. By comparing observed networks to null models, non-social factors which influence the associative behaviour of animals can be accounted for (e.g. home range overlap, temporal effects, etc.) and specific hypotheses about social processes can be tested (VanderWaal et

al. 2014a; Adelman et al. 2015; Farine 2017). To test if bond strength in each observed network was significantly different from what would be expected by chance (hypothesis i), the mean SRI and CV values for the observed network were compared to a distribution of mean SRI and CV values generated using 1000 permutations of the network data (Manly 2006). We used pre-network data permutations as these types of null model can account for inherent structure in the observed data, and are the most reliable at detecting real effects i.e. they reduce type I and type II error rates; see Farine (2017) for a full review. Our null models controlled for sampling period and spatial distribution of individuals to ensure that the distribution of individuals in the null models remained consistent with the patterns in the observed data. This accounts for the influence of any space-related factors (i.e. individual home ranges, habitat type or space use) and sampling-period factors (weather, resources abundance) and creates a null model in which the structure of the data (space and time) are retained, but individual variation is not (Aplin et al. 2015; Spiegel et al. 2016; Muller et al. 2018b). This ensures that the only process which is randomised is the process of interest, i.e. the social associations - who is observed with whom - and allowed us to make inferences about social organisation independent of temporal or spatial variables. To control for effects of spatial distribution, we split the study area into 40 grid squares, each measuring 0.1 latitude x 0.02 longitude and data swaps in the null model were restricted to within each spatial grid, so that data were only swapped between individuals that were observed in the same location during the same time period (Aplin et al. 2015). The observed variance in latitude and longitude were 0.8 and 1.1 of a decimal degree respectively.

A *p*-value was obtained by comparing the observed mean SRI and CV value to the distribution of the mean SRI and CV values from the 1000 random networks (*p*-values stabilised after ~200 permutations of the observed data, so 1000 permutations was sufficient to ensure the *p*-values were representative). To assess how the other network measures (density, clustering coefficient, path length) differed between the two networks (SC and LNNP), we compared the network-level observed mean values between populations. We did not test these using null models for the

following reasons: i) SRI and CV permutations are the most effective values to establish if the observed networks are non-random (Whitehead 2008; Farine & Whitehead 2015); ii) density and bond strength would have been the same as the null model (Belton et al. 2018); and iii) our hypotheses focus on the differences between the network structure of the two populations, not their comparisons to random *per se*. All analyses were performed on all four networks: whole and filtered (calves excluded) for each study site.

3 RESULTS

3.1 Patterns of association

The SC and LNNP whole networks are visualised in Figures 2 and 3 respectively. The whole SC network contained 1861 connected dyads and 695 unconnected dyads; after filtering out calves, there were 1059 connected and 216 unconnected dyads. The whole LNNP network contained 2405 connected and 1511 unconnected dyads; after filtering out calves, there were 2331 connected and 1155 unconnected dyads. The mean number of associates per individual for each whole network was 51.7 in SC and 54.0 in LNNP. When calves were removed, this fell to 41.5 in SC and was little changed, at 55.5, in LNNP. Since there were 50 adults/subadults and 22 calves in SC, and 79 adults/subadults and 5 calves in LNNP, most individuals in each population encountered each other during the study period.

Both networks were non-random; in all cases (both study sites, whole and filtered networks) the observed mean SRI and mean CV value were significantly greater than would be expected by chance, based on corresponding values from the null models (Table 1).

3.2 Network metrics

In both the whole and the filtered networks, density, clustering coefficient and path length were all higher in SC compared to LNNP (see Table 2). Within networks, all metrics increased when calves were removed.

4 DISCUSSION

Association patterns in both populations were significantly different to those that would be expected by chance, indicating that giraffes showed preferences to associate with and avoid specific individuals (Whitehead 2008). This supports the results of previous studies suggesting that giraffes live in social groups with familiar individuals (Bercovitch & Berry 2013a; Carter et al. 2013b), and suggests that the mechanisms driving individuals to associate with preferred conspecifics are not completely disrupted by high levels of disturbance by humans and predators. Currently there is considerable uncertainty over how giraffes choose to associate with conspecifics; the available evidence suggests that they group with others based on kinship, age, individual preferences or behavioural state (Bercovitch & Berry 2013a, b; Carter et al. 2013a, b; Muller et al. 2018b), and that shared space use plays a significant role in association patterns (Carter et al. 2013b; VanderWaal et al. 2014a). Our null models controlled for the spatial and temporal distribution of individuals, ensuring that the only element randomised was the association patterns between individuals. Since this removed any obvious factors which might confound our assessment of association choices, such as shared space use, sampling bias or habitat type, we can say that giraffes show non-random patterns of association independent of spatial or temporal variables.

Individuals in the area with low disturbance (SC) had stronger and more exclusive bonds (i.e. higher SRI and CV values) than those in the area exposed to high disturbance (LNNP) (hypothesis i). When calves were removed from each network, mean SRI increased (SC) or remained stable (LNNP) but the CV in both networks decreased. This suggests that the presence of calves weakens measures of bond strength at a network level. It could be that the presence of calves is not important for maintaining higher and more exclusive bonds at a network level, but this is more likely to reflect changes in the association patterns of mothers, which then contribute to the overall network means.

Measures of whole network structure generally supported our predictions and indicated that the network exposed to high disturbance was more fragmented than the network with low disturbance.

Fewer potential associations between individuals were realised (lower density) under the high disturbance (hypothesis ii). This indicates that the network is more segmented and individuals exhibit fewer social interactions between groups. This may be because individuals are forced to disband due to human- or predator-related disturbance, or that they cannot use the habitat as freely as those in SC, due to restrictions on space used imposed by human-related development, roads that are busy with high levels of tourist traffic throughout the area, or through avoiding areas which lions occupy. The network under high disturbance showed less connectivity (lower clustering coefficient; hypothesis iii) than the network under low disturbance, which, like density, may indicate the network is fractured with isolated sections and groups of individuals. We found shorter path length under high disturbance (hypothesis iv), which could be indicative of the more temporary nature of connections, as suggested by the low bond strength (edge weights). In LNNP, low path length could indicate the presence of smaller, more isolated groups which are not as strongly bonded as those in SC. Networks with small path lengths, all other things being equal, have a quicker spread of disease and information (Reppas et al. 2012), so perhaps shorter path lengths in areas of high pressure are beneficial, since information about disturbance or threat can be transmitted more quickly. The lower mean edge weight for giraffes in LNNP would support the possibility that giraffes are disbanded and moved between groups in LNNP more often than in SC.

While social networks can confer fitness benefits to individuals, it is not so clear what consequences arise from the disruption or disturbance of such mechanisms. In humans, poor access to social networks is associated with ill health and poverty (Belle 1983; Cattell 2001; Adato et al. 2006), but the effects of poor social integration have not been explicitly tested in other species. Given that, close bonds of adults and stable social structure have been shown to increase fitness and survival of offspring in multiple taxa (Silk et al. 2003, 2009; Cameron et al. 2009), it is plausible that the opposite means fitness reductions and reduced birth rates and survival of offspring. So, the low cohesion and high fragmentation of the network in LNNP could have fitness implications for that population. Coincidentally, the giraffe population in LNNP has very few calves (Muller 2018). This

404 was attributed to the high predation by lions (Brenneman et al. 2009), an obvious conclusion given
405 that lion predation of giraffe calves is known to be high (58% of calves < 1 year in Tanzania are killed
406 by lions (Pellew 1984; Strauss & Packer 2013), and because LNNP contains a high density of lions
407 (Ogutu et al. 2012; Muller 2018). But if high predation by lions is the proximate cause of the lack of
408 calves in the LNNP population, what is the ultimate cause? One hypothesis is that if social networks
409 offer survival benefits to young, and those social networks are disrupted (potentially by high levels
410 of disturbance, as demonstrated in hyaenas; Belton et al. 2018), could this disruption result in
411 reduced survival of young? It is well established that stable social networks facilitate the survival of
412 the young (Silk et al. 2003, 2009; Cameron et al. 2009; Stanton & Mann 2012; Brent et al. 2015,
413 2017; Goldenberg et al. 2016; Lahdenperä et al. 2016), so it seems plausible that disruption of those
414 networks could influence calf survival, and potentially explain the lack of calves in LNNP. There is
415 evidence of alloparental care in giraffes; young calves are frequently left in a crèche system, cared
416 for by adults other than their mother (Leuthold 1979; Pratt & Anderson 1979, 1985), there are
417 several reports of allonursing (Pratt & Anderson 1985; Perry 2011; Gloneková et al. 2016, 2017) and
418 females express distress behaviours following the death of another individual's calf (Bercovitch
419 2012; Strauss & Muller 2013). The presence of social bonds between adults may therefore be
420 important to facilitate the survival of calves, so the disruption of those bonds across the population
421 in LNNP may have adversely affected the survival of calves.

422 An alternative hypothesis is that high lion predation was responsible for the removal of calves, and
423 the lack of calves contributed to bond disruption in females. Maintenance of a high mean bond
424 strength before and after filtering calves out of the network suggests that strong bonds exist
425 between adults, and that mother-calf bonds are not the sole contributor to high mean bond
426 strength at a network level. Disruption of social structure can have a severe impact on wider
427 population processes within social species (Manor & Saltz 2003), making it possible that disruption
428 of the giraffe network in LNNP has negatively affected the survival of calves. Understanding which
429 comes first is a difficult question to answer: do strong bonds between adults lead to increased calf

survival, or does the presence of calves facilitate strong bonds between adults? Understanding the direction of such social processes, how these vary between species, and the implications for the success of individuals remains a central question in biology.

We also recognise that observed differences in network structure between our two study populations were due to factors other than levels of disturbance. For example, differences in the relative availability of conspecifics between the two sites (population demography; Muller 2018) may have influenced patterns of associations. Likewise, local differences in habitat structure and forage availability may have been influential but were outside the scope of this study. We highlight these limitations so that our results can be interpreted in the correct context, and so that future work can consider these aspects in their study design. We also recognise that studies like this would be able to draw stronger conclusions if networks structure could be linked to fitness and survival outcomes, but will require much longer-term data sets than we were able to collect.

5 CONCLUSIONS

We have demonstrated how the social networks and association patterns of the same species can be very different between populations, despite using the same study design, observer, data collection methodologies and analytical techniques. Such disparity in network structure between two populations suggests caution in drawing general conclusions about a species' behaviour from studies which focus on a single population. The comparison of networks has provoked some discussion (Faust & Skvoretz 2002; Faust 2006; Dubé et al. 2008), but we demonstrate its value in understanding how key environmental variables may influence the natural behaviour of species. We have demonstrated how the latest techniques in generating null models against which to test our hypotheses can be used to account for spatial and temporal factors, enabling the identification of true patterns of social preference. Studies of social behaviour which do not account for environmental factors in null models must be interpreted with caution, since social processes have not been isolated from the influence of external variables (Farine 2017).

As wildlife populations become increasingly restricted to enclosed conservation areas, and wildlife tourism continues to experience significant growth, it is critical to understand how human activity and associated disturbance affect the social behaviour of wildlife populations. Further, as wildlife populations become increasingly enclosed and prey populations are confined to areas containing high predator density, we need to understand how this may influence social networks, which in turn might have an impact upon population dynamics and demography. We have provided evidence to suggest that disturbance by humans and predators may be disruptive to the social networks of giraffes, and introduce the hypothesis that such disruption is a contributory cause of reduced calf survival in LNNP. If this hypothesis is true, it raises difficult questions about balancing the need for species conservation and protection alongside commercial activities which support conservation, and the conservation of large predators alongside threatened prey species (Bercovitch 2018). We suggest that further work is needed to understand exactly how disturbance by humans and predators influences the social behaviour of animals, but more importantly, how subsequent changes in animal behaviour influence the survival, reproduction and evolution of those species. We also hope that our findings will serve as a caution to other researchers about the danger of drawing general conclusions about the social organisation of a species based on single-population studies, and act as a catalyst to promote wider discussion about the challenges and benefits of comparing networks.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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TABLE 1 Mean non-zero edge weight (using the simple ratio index, SRI) and coefficient of variation (CV) values for the observed and random networks for both study sites (Soysambu Conservancy, SC, and Lake Nakuru National Park, LNNP) including all the network data ('whole network') or without calves ('filtered network'). Significance was tested at the $P < 0.05$ level, based on 1000 random network permutations

	Observed network	Random network	P value
SC: whole network			
Mean SRI value	0.125	0.083	<0.001
Mean CV	116.938	75.373	<0.001
SC: filtered network			
Mean SRI value	0.126	0.095	<0.001
Mean CV	95.081	64.118	<0.001
LNNP: whole network			
Mean SRI value	0.088	0.053	<0.001
Mean CV	130.369	93.768	<0.001
LNNP: filtered network			
Mean SRI value	0.088	0.056	<0.001
Mean CV	121.451	86.444	0.004

930 **TABLE 2** Network metrics for both study sites (Soysambu Conservancy, SC, and Lake Nakuru National

931 Park, LNNP) using network data including ('whole network') or without calves ('filtered network')

	Density	Clustering Coefficient	Path Length
SC: whole network	0.728	0.822	0.243
SC: filtered network	0.831	0.877	0.362
LNNP: whole network	0.614	0.757	0.219
LNNP: filtered network	0.669	0.767	0.243

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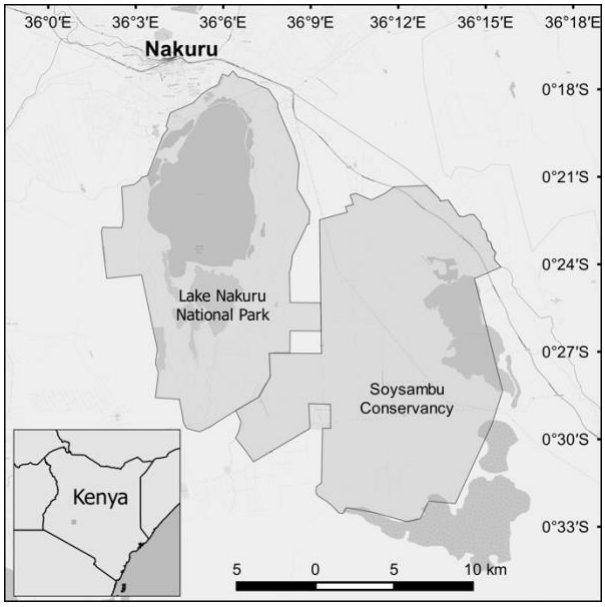
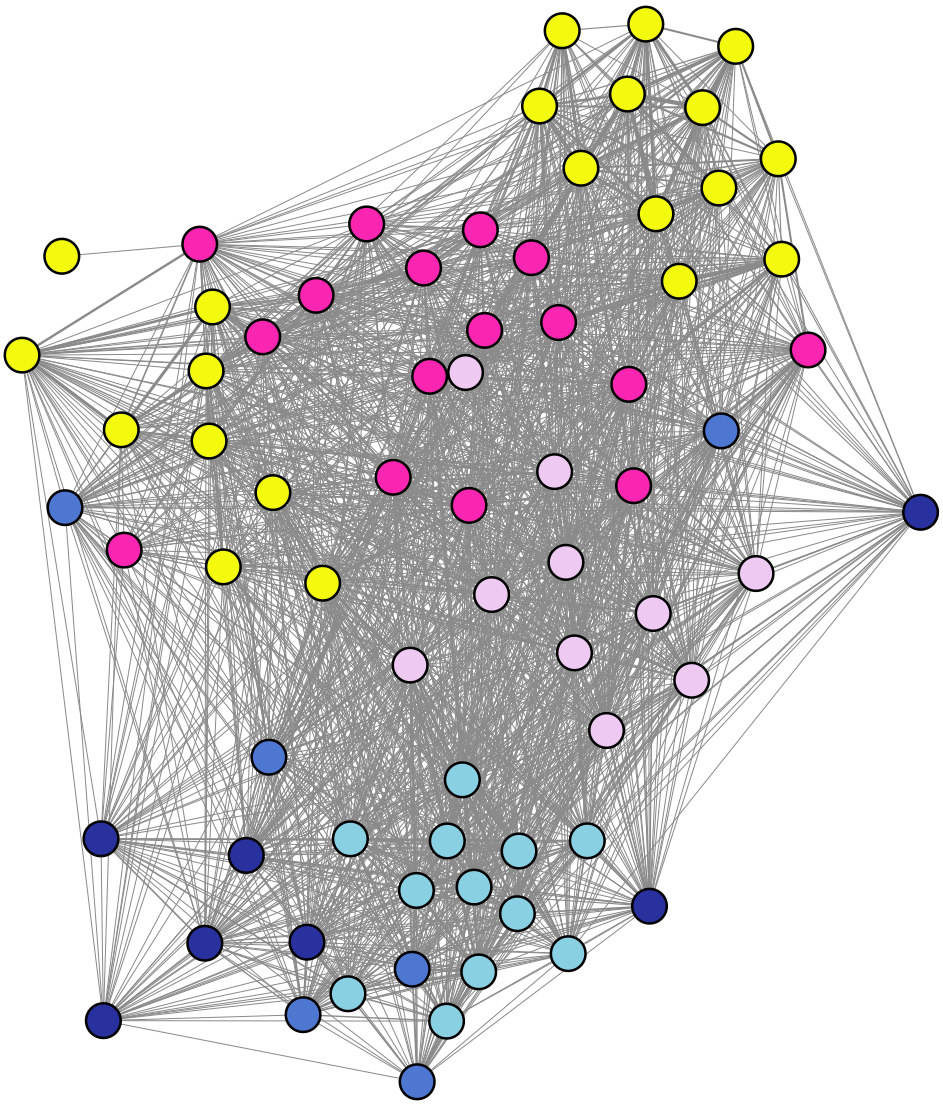
940 

941 FIGURE 1 Location of the study sites in the Great Rift Valley region of Kenya. Reproduced, with

942 permission, from Muller, et al. 2018. Journal of Zoology 306, 77–87. Base map provided by Google

943 Maps 2018.

944



945

946 FIGURE 2 Visualisation of the whole network in SC. Nodes are coloured by sex: mature bulls = dark
947 blue; adult males = mid-blue; subadult males = light blue; adult females = dark pink; subadult
948 females = light pink; calves = yellow. Edges are undirected and weighted by the association index
949 (Simple Ratio Index); darker lines represent stronger relationships between individuals.

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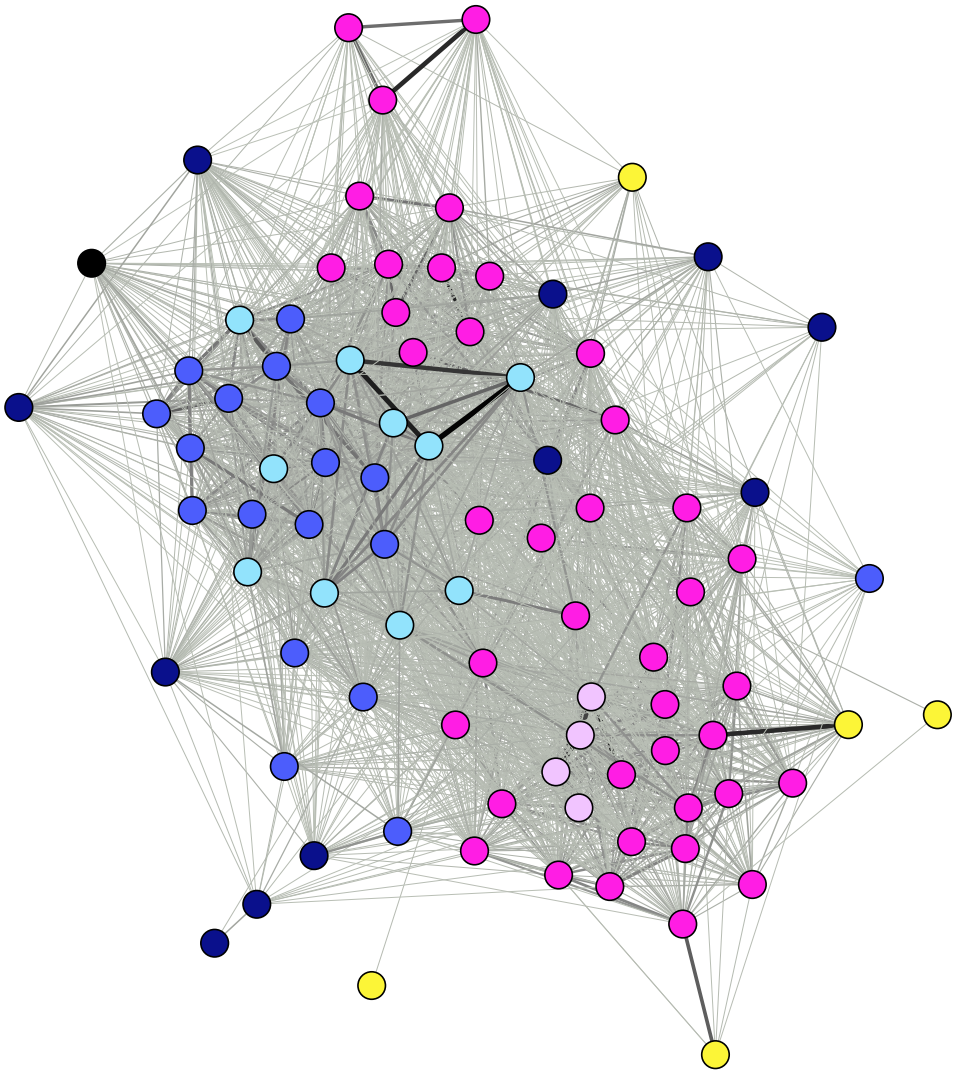

951

952 FIGURE 3 Visualisation of the whole network in LNNP. Nodes are coloured by sex: mature bulls =
953 dark blue; adult males = mid-blue; subadult males = light blue; adult females = dark pink; subadult
954 females = light pink; calves = yellow. Edges are undirected and weighted by the association index
955 (Simple Ratio Index); darker lines represent stronger relationships between individuals.

956